

and three quarter times the length of the combined head and trunk. The head, about half of which is formed by the long needle-like beak, is at least twice the length of the trunk proper; its posterior half is broad, deep, and subquadrangular. Eyes minute, subcutaneous, without any orbital fold. The maxillary teeth are arranged in a single row, and diminish in size but increase in number from behind forwards: the vomerine teeth posteriorly are long and sharp and are disposed in a long, close-set, comb-like series; anteriorly they form a fine rasp-like band: in the mandible a row of large distant needle-like teeth stands up from an uneven band of small denticles. Gill-openings close together, wide. The scaleless integument is thin and deciduous and thickly enveloped in mucus; no lateral line is apparent. The dorsal fin is feebly developed, and, indeed, hardly distinguishable. The pectoral fin is represented by an inconspicuous clavicular knob, without any rays.

The abdominal cavity extends at least halfway along the tail. The siphonal stomach, which has its pyloric end long, tapering, and much constricted, leads into a widely expanded duodenum, which, in the single specimen dissected, is furnished with a small diverticulum near the pylorus.

Colour uniform black, with a silvery sheen on the head.

This species is perhaps identical with *Nemichthys infans*, Vaillant (nec Günther), described and figured in Expéd. Sci. du 'Travailleur' et du 'Talisman,' Poiss. pp. 93 and 94, pl. vii. fig. 1, and there only doubtfully referred to Dr. Günther's type.

EXPLANATION OF PLATE XVIII.

Fig. 1. *Hepthocara simum*, sp. n.

Fig. 2. *Alepocephalus edentulus*, sp. n.

Fig. 3. *Xenodermichthys Guentheri*, sp. n.

XLI.—On the Origin and Development of the Mammalian Phylum. By Dr. W. KÜKENTHAL*.

[An Address delivered on May 28, 1892, in the Aula of the University of Jena, in accordance with the provisions of the Paul von Ritter foundation for phylogenetic zoology.]

OWING to the great division of labour which has taken place in our science, compelling the investigator to occupy himself with individual problems, it is well that we, for once allowing

* Translated from the 'Biologisches Centralblatt,' xii. Bd. no. 13 (15th July, 1892), pp. 400-413.

our gaze to range further afield, should consider the relation of the separate contribution to the great whole, and from these general considerations should derive new ideas, or in some sort form plans, to guide us in our future work. It often happens that these ideas are widely different from that which one day appears as the result of laborious individual investigation in the same direction. If, however, we are justly conscious of this difference, we may well venture to give utterance at some time to such ideas, especially if, as on this annually recurring occasion, we are not in a position always to adduce verified results of our own original work, such as might engage the attention of a larger circle of listeners.

From this point of view I would ask you to consider my deductions on the subject of the Origin and Development of the Mammalian Phylum.

Of all Vertebrates, Mammals are the last to appear upon the earth; we find their earliest remains scantily represented in Triassic formations. While they very soon secured the mastery for themselves, so that we may designate our geological period as that of the Mammals, before their appearance the phylum of the Sauropsida was predominant. It is therefore quite natural to commence with the consideration of the latter if we would make a closer acquaintance with the question of the origin of Mammals.

We can gain no idea of the extraordinary wealth of forms in the reptilian class by considering the lizards, snakes, chelonians, and crocodiles which are at present in existence. These are merely the last miserable shoots of a once far-spreading tree, which embraced more than double the number of orders; we can gain no comprehensive view of them until we examine the remains which the strata of the earth have preserved for us. On the basis of the palæontological discoveries which multiply from year to year, we are enabled to trace the phylogeny of the reptiles, at least in its main outlines, with tolerable certainty.

The Reptiles, which did not appear on our earth until after the Fishes and Amphibia, have their earliest known representatives in the Permian formation, which belongs to the Palæozoic period. The Progonosauria, as they are called, are types which have as yet undergone but little specialization and combine in their organization the characteristics of all other orders of reptiles. Like a relic from remote antiquity, a descendant of these old forms projects into the present, represented by the genus *Hatteria*, which occurs only in New Zealand.

Almost simultaneously with the Progonosauria, and allied

to them in its earliest representatives, a second order appeared, that of the Theromorpha, which exhibits an extraordinarily many-sided development, and to which we have to devote closer attention. Likewise referable to the Progonosauria are the two orders Sanropterygia and Ichthyosauria, which enjoyed a pelagic existence upon the open sea and have undergone profound transformations in their structure, quite analogous to those which at a later epoch of the earth's history were experienced by the whales among the mammals. Very old also is the order of the Crocodilia, a branch of which has been preserved until the present time. In consequence of the palæontological facts their phylogeny is considered to be very well understood. The earliest crocodiles are Triassic; then forms greatly changed in aspect reappear in the uppermost Jurassic formation; these are traceable through all subsequent strata up to the present time. Now it is highly instructive to see how incomplete are even the best palæontological records, for, on the basis of embryological investigations upon crocodiles, I am driven to conclude that their ancestors were at a certain time pelagic animals * with corresponding characteristic morphological peculiarities, and only gradually developed into the littoral and fluviatile creatures such as we find them to-day. Palæontology, however, has no knowledge of such pelagic ancestors; its attention is first directed thereto by means of embryology, and it is to be hoped that we shall one day succeed in finding remains of the supposed ancestors in the strata which precede the uppermost Jurassic series. With the oldest crocodiles as well as the Progonosauria (Rynchocephala) there is connected an order which excites general interest owing to the fact that it contains the largest terrestrial forms that the earth has ever produced. The length of the American *Atlantosaurus*, for instance, amounted to 115 feet, and its height to 30 feet, while its thigh was more than 6 feet long, and at its upper end exceeded 2 feet in diameter. Since these animals employed exclusively the hind legs for walking, a transformation of the hinder extremities, as also of the pelvis, was produced owing to the transference of the weight of the body to them, just as we see is the case in the birds in consequence of the same physiological cause. In spite of the fact that we may not at once utilize such resemblances for the purpose of establishing a phylogenetic connexion between the two, it is nevertheless conceivable that Dinosauria and birds may have

* In a paper which is at present in the press I have endeavoured to prove this assertion by means of the embryology of the skeleton of the hand.

common ancestors. In any case the birds have nothing to do with the order of the flying reptiles to which the remarkable *Pterodactylus* belongs. The origin of the Pterosauria is as yet by no means elucidated. While the Chelonians are a strongly specialized branch, which is perhaps to be derived from a group of the Theromorpha, the Lacertilia have their root in the primeval Rhynchocephala. From them there branched off during the Cretaceous period the pelagic Pythonomorpha, which soon became extinct again, as also the snakes, which are still in existence.

Having thus given a brief outline of the phylogeny of the Reptiles as it is now pretty generally accepted, we must now proceed to inquire from which of their orders the phylum of the Mammalia can have sprung. To this question an answer has been given to the effect that the already-mentioned Theromorpha are regarded as ancestors of the Mammalia, since they exhibit the greatest similarity to them. As a matter of fact a comparison of the skeletons, according to which alone we can proceed, since no other remains have come down to us, exhibits a considerable number of similar characters in the two groups*.

Especially striking is the oft-quoted resemblance in the differentiation of the dentition. As among the Mammalia, so also in the Theromorpha, we find a morphological difference within the dental series; here also we may speak of incisors, canines, and molars, in contradistinction to other reptiles, in which only uniformly conical teeth exist in the jaw. It therefore appears to be imperative that we should undertake a closer consideration of the Theromorphous dentition.

Of the four suborders of the Theromorpha the greatest number of resemblances in dentition to other reptiles is exhibited by the Pareiasauria. In these creatures all the teeth, the number of which was fairly large (seventy-six in *Pareiasaurus bombidens*), were devoted to tolerably similar functions, and accordingly exhibit only small differences in their structure. In all the genera described by Owen (*Tapinocephalus*, *Pareiasaurus*, and *Anthodon*) distinct rudiments of successional teeth are present internally to the dental series.

Far greater differentiation is found in the dentition of the Theriodontia, whose teeth are constructed according to the carnivorous type. No trace of rudiments of successional teeth has been found in any of these predaceous reptiles.

The two other suborders have a dentition which is very

* Cope, "The Relations between the Theromorphous Reptiles and the Monotremata Mammalia," Proc. Amer. Assoc. for the Advancement of Science, vol. xxxiii. (1885).

divergent in form; the Anomodontia possessed only a pair of powerful tusks (similar to those of the walrus) in the upper jaw, or were completely edentulous.

The Placodontia, whose right to be included in the order of the Theromorpha is, however, not certain, were still more singularly equipped, since they possessed incisors in front, and posteriorly rounded molars in the upper jaw and large flattened teeth in the mandible, while in addition to these the palate was covered with large flattened teeth. A precisely similar dentition is found, moreover, in fossil fishes—the Pycnodontia—to which these reptiles were at first assigned.

If we disregard for the moment the two last-mentioned groups, and devote our attention to the Pareiasauria and Theriodontia, we are especially struck by the fact that here we are not confronted, as in the case of other reptiles, with a succession of several dentitions, which are capable of excellent preservation in fossils (compare, for instance, the figure of *Diplodocus longus*, Marsh, in Zittel's 'Handbuch der Paläontologie,' iii. Bd. p. 716, where no fewer than six consecutive successional teeth are developed); but that in these animals there takes place only a single succession or none at all—the latter being the case in the most specialized dentitions. Within the order of the Theromorpha therefore the formation of successional teeth is lost as the individual teeth become more highly specialized.

We meet with perfectly analogous conditions once more in the mammals*, for in the marsupials also the second dentition is suppressed with the exception of one premolar, although it is present in the form of a rudiment (the dental fold); here also the teeth of the first dentition, which alone arrives at development, are highly specialized.

A very material advance in the completion of the dentition is not exhibited until we come to the placental mammals, in which (with a few exceptions, which will be dealt with directly) highly specialized teeth of the second as well as of the first dentition are developed. With this we have attained the highest known stage of dental development. As regards the exceptions, the toothed whales and the edentates, I have already shown in my address delivered on this occasion last year, that the condition of their dentition is a secondary one, since the primitive specialization of their teeth appeared no longer necessary, in consequence of diminution of their diffe-

* *Vide* my papers in the 'Anatomischer Anzeiger,' 1891, pp. 364 and 658 [Ann. & Mag. Nat. Hist. ser. 6, vol. ix. pp. 279-294], as well as my address delivered on May 30, 1891, "Ueber den Ursprung und die Entwicklung der Säugetierzähne," Jenaische Zeitschrift, 1892.

rent functions, and the second dentition which was originally present is still developed rudimentarily in the embryo, but no longer cuts the gum. The similarity between the dentition of these two orders of placental mammals and that of the marsupials is therefore due to the persistence of the first dentition ; but the great difference is that in the case of the marsupials the second dentition does not appear, because the teeth of the first have become highly specialized, while in that of the edentates and toothed whales the same phenomenon is occasioned by a degeneration produced by a diminution of the functions.

If we therefore consider impartially the groups which we have been discussing, not allowing ourselves to be prejudiced by phylogenetic hypotheses, we see that in Theromorpha, marsupials, and placental mammals the original condition of the dentition was that of polyphyodontism in the case of the first-mentioned group and diphyodontism in that of the two latter. But we further find that in consequence of the same cause, specialization of the individual teeth, in the Theromorpha all dentitions except the first were suppressed, while in the marsupials at least one tooth of the second dentition became functional ; but in the placental mammals, in spite of the specialization, both dentitions appeared.

In the three groups of the Theromorpha, Marsupialia, and Placentalia we thus have three stages in dental development which differ in height and which have been developed according to the same laws, but from a successively higher basis.

The impression is produced upon us that the height of the development of the dentition always corresponds to the degree to which the organization of the groups of animals in question has advanced, an idea which is rendered perfectly probable owing to the principle of correlation of organs. This is as much as to say that the similarities which we find in the three differently advanced forms of dentition depend upon phenomena due to convergence, and cannot be employed to set up phylogenetic connexions. As a matter of fact we see that the dentition of the Theriodontia really resembles that of the predaceous Marsupialia and predaceous Placentalia, but not that of the lowest mammals, with which we are acquainted owing to the discoveries of palæontology, and to the consideration of which we will now proceed.

The oldest known remains of mammals come from the Trias and exhibit a wide geographical distribution, since isolated teeth or incomplete skulls have been found in Swabia, in North Carolina, in Basutoland, and at the Cape. This by itself is an argument in favour of greater antiquity for the mamma-

lian phylum, and renders it probable that the group had its origin in the Palæozoic period. In the examination of the Triassic mammals we have to rely almost exclusively on the teeth, the structure of which is extremely peculiar. It is true that in many respects they still have a reptilian character, which is especially visible in the small development of the root; but not only do we find a specialization of the dentition into incisors, canine, and molars, but the structure of the latter is in the highest degree remarkable, for each molar is composed of numerous cusps, which are arranged in two or three rows and are separated by longitudinal furrows. In consequence of this the name "Multituberculata" has been bestowed upon these ancient mammals.

A year ago I advanced the theory that the molars of the Mammalia are to be regarded as having arisen owing to the fusing together into groups of original conical reptilian teeth*, and this conception was chiefly derived from the observation of the contrary process, since in whalebone whales a large number of teeth with single tips is produced from original multicuspid molars through fission, which sets in in the course of the development. Now in the molars of the Multituberculata I find an important argument in favour of my view. I regard a molar of one of these mammals as having arisen through the fusion of a number of conical reptilian teeth, and, simultaneously with this, a fusion of the corresponding successional teeth with one another and the first series. In the case of the multituberculate molars, which are provided with three longitudinal rows of cusps, a fusion of corresponding teeth of the third dentition is superadded. The fusion of teeth belonging to successive dentitions is in itself in no way wonderful. The difference in the time of appearance is indeed an absolutely secondary phenomenon, and in the highest

* This idea, which was suggested by me with the necessary reserve, was rejected as infelicitous by O. Thomas ("Notes on Dr. W. Kükenthal's Discoveries in Mammalian Dentition," *Ann. & Mag. Nat. Hist.* ser. 6, vol. ix. no. 52, p. 312), who, in doing so, relies chiefly upon the fact that the number of teeth in the primitive Mammalia is greater than that which is found in many Anomodontia, the most mammalian of the Reptilia. "This fact is alone sufficient to discredit Dr. Kükenthal's theory." Although now as ever I am far from regarding my idea as a thoroughly substantiated theory, I would nevertheless here point out that after what I have stated above as to the position of the Theromorpha it is impossible for me to admit this objection. In an essay which has appeared during the printing of this paper ("Ueber die Entstehung der Formabänderung der menschlichen Molaren," *Anat. Anz.* June 3, 1892) Herr Röse adopts my conception, and designates it as his theory, without even mentioning me, although he is acquainted with my papers on this subject.

mammals also a fusion of the rudiments of both dentitions occurs in the formation of the true molars*.

If the multituberculate molars have arisen in this fashion, it follows that their number must be very small, since each tooth corresponds to a whole series of simple reptilian teeth. As a matter of fact we find in each half of the jaw only one or two molars, while the number of the similarly constructed premolars is at the most four, but usually less. It is difficult to understand how the process of fusion has taken place, since the shortening of the long jaws of the reptiles to the short ones of the mammals is not of itself a sufficient explanation; nevertheless the fusion of teeth in the vertebrates is a fact, and consequently my view is in no way opposed to processes of tooth-formation in lower Vertebrata.

If the mammalian molars have really arisen as I have suggested, the hypothesis which is at present generally accepted, and has been especially developed by Cope and Osborn, is consequently invalidated up to a certain point. Starting from the simple conical reptilian tooth, such as, according to these authors, has been preserved in the dolphin†, the development of the mammalian molars is supposed to have taken place by the outgrowth of a small cusp in front and behind. The difficulty of conceiving the mechanical process of such an outgrowth has already been touched upon by Fleischmann‡, since Cope's attempt to explain the development of these cusps, as being due to the increased supply of formative material, is an absolute failure. But the difficulty is abolished if the triconodont and tritubercular teeth are regarded with me merely as constituting a special division of the multitubercular teeth, and therefore as structures which

* This view also, which I expressed on the basis of my investigations, is regarded by Thomas (*loc. cit.* p. 311) as an "extraordinary and, to all appearance, most unlikely theory." Without here entering into further explanations, I will merely refer the reader to p. 231 of Hertwig's 'Lehrbuch der Entwicklungsgeschichte des Menschen und der Säugetiere,' where it is stated:—"In addition to this the enamel organs of the posterior or true molars, which are subject to no change, but of which the rudiments are altogether only formed once, are developed at the right and left end of the two epithelial folds." These two epithelial folds are, however, nothing else than the earliest rudiments of the enamel organs of the first and second dentition, which in the case of the premolars remain separate.

† Thomas is in error in thinking that this view is only shared by Baume; *vide, e. g.*, Schlosser, "Die Differenzierung des Säugetiergebisses," *Biol. Centralbl.* 1891, p. 238.

‡ Fleischmann, "Die Grundform der Backzähne bei Säugetieren und die Homologie der einzelnen Höcker," *Sitzungsber. der k. Akad. Berlin*, 1891.

have originally arisen through fusion. The further hypotheses of the American palæontologists, in connexion with the tritubercular type of tooth, are not affected by this.

A radical distinction would consequently have to be drawn between the molars of the reptiles and those of the mammals. The teeth of the theromorphous reptiles, whose molars were already described by Owen in most cases as simple conical teeth, are only homologous to a simple reptilian tooth, or else, as in the case of the Theriodontia, a fusion takes place. This fusion, however, always affects the individual tooth alone, and the rudiment of its corresponding successional tooth, which is contained in the dental fold. (My view is clearly illustrated by the figure of the skull of *Empedocles molaris*, Cope, given by Zittel in his 'Handbuch der Paläontologie,' Bd. iii. p. 581.) The molars of the Mammalia, on the other hand, represent much more complicated structures; they have arisen through the fusion of a larger or smaller number of conical reptilian teeth which lie one behind the other, and in addition to these there is usually added the corresponding series of teeth of the second and it may be of the third dentition. In this process the shortening of the jaws must have had an important mechanical effect.

I would further support my hypothesis by the following consideration, which also embraces the other classes of Vertebrata. *In the first place I lay down this principle for the development of the teeth within the entire vertebrate series, that the development of the dentition is primarily traceable to the fusion of individual teeth.*

The simple dentine tooth of the fishes is to be regarded as the primary element. Just as, according to O. Hertwig, the covering bones of the oral cavity have arisen through the growing together of the basal plates of these elementary structures, so also through fusion of the teeth themselves more complicated forms of teeth have been produced.

This process can be traced by means of comparative anatomy in the Selachians. Thus, for instance, *Cladodus*, one of the oldest forms of sharks, exhibits the following arrangement of teeth: on an elongated base a number of conical tips arise, of which the middle and the two outer ones are the longest (*vide* Zittel, Bd. iii. p. 67). The origin of this dental structure would be quite unintelligible if we would assume it to have arisen through gradual differentiation of a single tooth-tip; it appears, on the other hand, quite natural to suppose this formation to consist of a series of individual teeth fused together. The other forms of teeth then arose through the more and more intimate fusion of the

individual elements. This, however, by no means excludes the possibility of individual teeth increasing in size, even without fusion, in consequence of having an increased amount of work to do; only the teeth with a number of tips cannot be thus explained. I therefore consider the original single tooth of the fishes as a tooth of the first order, as opposed to the teeth of the second order, which have arisen through the fusion of several, as we already find them within the class of fishes. With this complication there naturally takes place a diminution in the number of dentitions of which rudiments are formed. In fishes tooth-change as a general rule is unlimited; it already ceases, however, within the limits of this class with the development of very large individual teeth, therefore with commencing specialization (*e. g.* in *Chimæra* or *Ceratodus*).

In reptiles also the number of dentitions is a limited one. If we would compare the individual tooth of a reptile with the teeth of fishes we should preferably select the teeth of the second order in the case of the latter. Like these many reptilian teeth also exhibit complications, which point to a fusion having formerly taken place (*e. g.* the teeth of *Scelidosaurus Harrisoni*, Owen [Zittel, Bd. iii. p. 741], or of *Anthodon* or *Galesaurus* among the Theromorpha).

Yet another fusion took place on the origin of the mammals from reptile-like ancestors. The mammalian molars are therefore teeth of the third order, which have arisen through fusion of reptilian teeth. The result of this process is seen most beautifully developed in the case of the Multituberculata, the oldest mammals which are as yet known.

A simple tooth of a fish and reptile and a mammalian molar are therefore not homologizable with one another; on the contrary, they represent three different stages of dental development proceeding from fusion. This at the same time gives us the simple mechanical cause of the gradual reduction of the dentitions.

The principle of fusion of teeth consequently explains the constant increasingly higher development of the dentition within the vertebrate series. A second principle, operating within each individual group, is that which modifies the teeth so as to make them as efficient as possible, and adapts them in accordance with the claims of function. Function depends upon the mode in which food is acquired; this, however, varies but little in the different classes of animals, and thus is explained the great similarity also which exists between the dentitions of many forms belonging to different classes of vertebrates, such as, for instance, is found in Theriodontia,

predaceous marsupials, and predaceous placental mammals. It consequently follows from my line of argument that a phylogenetic connexion between the forms in question on the basis of the dentition is absolutely inadmissible.

The question as to the origin of the Mammalia we now answer in the following way. The ancestors of the Mammalia were not theromorphous reptiles, as is usually supposed, but primeval forms (from which indeed the Theromorpha may likewise have originated) living during the Palæozoic period, with a but little specialized dentition, which still consisted of uniform conical teeth. From these there were developed in the first instance mammals with a multituberculate dentition.

Many suggestions may be made as to the causes which may have brought about the origin of the Mammalia. The statements of Haaeke * on this point sound quite plausible. According to this writer the mammals, which are warm-blooded in contradistinction to the reptiles, which have an alternating temperature, can only have originated at a time when the temperature underwent an appreciable and permanent cooling; and it is stated that this probably took place during a cold period, which geologists term the Permian (?) Glacial epoch. With the acquisition of a higher temperature for the blood, the development of a bad conductor of heat, in the shape of the hairy coat †, became necessary; and to this was added the formation of sebaceous glands to grease the hairs, and sweat-glands to regulate the temperature of the body.

Moreover, in connexion with the lowering of the temperature came the incubation of the ova, for the young had now to be hatched by means of the mother's own bodily heat. In relation with this we have the formation and further development of the incubatory apparatus, such as we still see it today in the case of the oviparous Monotremata.

We now come to the second part of our subject, that of the development of the mammalian phylum. The existing mammals are divided into three subclasses—Monotremata, Marsupialia, and Placentalia. The bodily structure of the still oviparous Monotremata, although variously modified in consequence of special adaptation, exhibits such primitive

* Haaeke, "Ueber die Entstehung des Säugetiers," Biol. Centralbl. 1889, p. 8.

† In a paper which will shortly be published, and which has been worked out under my direction, it will be proved by Herr Römer, one of my students, by means of embryological investigations, that the dermal armature of the armadillos is a secondary acquisition, and that in their original condition these animals were provided with a hairy coat.

characters that we must regard them as descendants of the most primitive mammals. Now, on the basis of our considerations on the dentition, we determined that the Multituberculata were the most primitive Mammalia; the Monotremata therefore must be the descendants of the old Multituberculata. This supposition recently received confirmation owing to the discovery that while the adults of both forms, *Platypus* and *Echidna*, are toothless, the young of the former possess two molars hidden beneath the flesh of the gum, which exhibit a distinctly multitubercular structure. The Monotremata therefore appear to be really a specialized lateral branch of the Multituberculata.

The representatives of the second subclass, the marsupials, branched off at a very early period from this ancient stem; their type of dentition is traceable to a modification of the multituberculate type. Their bodily structure exhibits in general a development occupying a position between Monotremata and Placentalia; and we regard them as an intermediate mammalian stage from which the placental mammals have been developed. According to many authors the several orders of placental mammals have sprung from the corresponding orders of marsupials, and the former are therefore polyphyletic in origin; according to others the subclass of the Placentalia originated from a more generalized marsupial type.

Let us now examine the evidence, which in any way goes to show that the placental mammals are to be derived from the marsupials. In the first place there are adduced general resemblances and the different degrees of development of the several organs. These arguments we can at once reject as untenable, for the different degree of the resemblance of the organs with those of the two other subclasses may be also explained, if we trace the placental mammals not to the marsupials, but directly to the monotremes. The resemblances would then be simply phenomena of convergence, arising in consequence of adaptation to a similar mode of life.

A more cogent argument for regarding the marsupials as the ancestors of the placental mammals would be the discovery of specific marsupial characters in the development of individuals belonging to the latter. Such a discovery is supposed to have been made in the finding of remains of the marsupial bones, which in the marsupials serve for the support of the pouch and are quite characteristic structures. Now, however, Wiedersheim*, the latest author on this

* Wiedersheim, "Die Phylogenie der Beutelknochen. Eine entwicklungsgeschichtlich-vergleichend anatomische Studie," Zeitschrift für wissenschaftliche Zoologie, liii., Suppl., 1892.

subject, writes as follows as to the persistence of the marsupial bones in the placental mammals:—"I must here at once observe that I have been unable to discover these in any embryo—and I have examined representatives of all the chief groups—to say nothing of an adult animal." That which persists in the placental mammals is a girdle of cartilage, which in the amphibians and reptiles represents the formative material of the epipubis, and in the marsupials furnishes the marsupial bones which are homologous with this.

If, therefore, the arguments in favour of the derivation of the placental mammals from the marsupial are untenable, there are, on the other hand, others which tell directly against the theory. The most primitive condition of the brood-apparatus is represented by two so-called mammary pouches, as they are found in the *Echidna*; the brood-pouch is an acquisition which is to be derived from this, in that the edges of the mammary pouches become completely (temporarily in *Echidna*) or partially (in the marsupials) fused together.

Now the dermal pouches which occur in many ungulates have recently been identified by Klaatsch* as mammary pouches, which he regards as discarded mammary structures, while the remaining pairs of mammary pouches have become completely modified into teats. Klaatsch therefore considers it to be conceivable that the ungulates never passed through a marsupial stage, and at any rate concludes that the ungulates have never possessed a pouch-structure like the existing marsupials.

A further weighty objection is to be found in the constitution of the dentition. As I was the first to demonstrate, the dentition of the adult marsupials belongs to the first series, while that of the adult placental mammals represents the second set of teeth. This by itself is at once a deep-seated difference which prevents any homologization. Moreover the marsupial dentition exhibits a type which is firmly closed within itself and from which a further development appears impossible. Quite characteristic is the entrance of a premolar of the second series into the dentition, a peculiarity which has persisted from the Jurassic down to the recent forms.

To sum up shortly the results of these considerations, we find that tenable arguments for deriving the placental mammals from the marsupials do not exist, but that there are some that tell against such a process. We may well imagine that the placental mammals originated from the ancient

* Klaatsch, "Ueber Mammartaschen bei erwachsenen Huftieren," *Morph. Jahrbuch*, Bd. 18, Heft 2, p. 349.

mammalian stem, which still persists with least alteration in the monotremes, and that certain of their orders have acquired the placenta independently of one another*. The marsupials form a branch which runs parallel to the placental mammals, and likewise originated from the main stem. The resemblances within the individual orders of the two subclasses are merely instances of convergence.

It is not my intention to follow out the development of the mammalian phylum in detail, enticing though it would be to show how the hypotheses derived from the study of comparative anatomy and embryology are supported by the palæontological discoveries which are multiplied from year to year. It was rather my desire to bring forward certain problems which are connected with the investigation of the mammalian phylum, and to expose the methods by which work is now-a-days carried on.

Far from regarding the erection of a sort of picture-gallery of ancestors as the goal to which our science should aspire, we rather seek to obtain a clue to the complicated causes which have brought about the immense variety of animal forms. We would discover the laws which the organic world obeys.

At the same time, however, I would wish to combat the fundamental error of believing the problem of life to be solved, if we should succeed in recognizing the mechanical laws which have been active in the development and modification of organic bodies. The knowledge of the vital processes themselves is not in the least advanced thereby; with the same degree of justice we could, to use Bunge's simile, regard the movement of the leaves and twigs on the tree, which are tossed by the storm, as manifestations of life. What we are able to perceive is nothing else than the way in which living matter reacts upon forces coming from without. This task, which has been attacked in its full extent by the physiology of to-day, has recently been claimed by a number of, for the most part, junior investigators as the sole object to which biological science has to devote itself. While claiming to have discovered an absolutely new method of biological investigation, they believe that this mechanico-etiological method is the only way which we dare follow for the solution of biological questions, and that the "morphologico-historical" method, based upon the theory of descent and hitherto generally employed, must be abandoned.

* Marsh represents the same view of the question on the basis of his palæontological investigations; *vide* Marsh, "American Jurassic Mammals," Amer. Journ. of Science, vol. xxxiii., 1887.

Indeed, in one direction they even talk of the "futility of the theory of descent"!

How could this view have arisen? In the first place it is to be remarked that the so-called "morphologico-historical" method is an artificially constructed conception, which by no means coincides with the "phylogenetic" method, which is nevertheless said to be intended thereby. It is undoubtedly true that morphology has stood for a time in the foreground and has been almost exclusively employed in phylogenetic investigations. Since in addition to this isolated branches of morphology were applied more or less exclusively to the solution of phylogenetic problems, our science threatened to become shallow. I need but allude to the innumerable papers in the domain of embryology which apply their one-sided results to phylogenetic speculations. A deepening of our science can only set in when not only the three branches of morphology, comparative anatomy, embryology and palæontology, but also physiology, are simultaneously employed as roads to knowledge. The goal which we thus attain to is the comprehension of the position of each animal in nature, the determination of its relations to the surrounding organic and inorganic world, and the discovery of laws of constantly more general application which have governed the organic genesis. Now, as ever, the problem of life itself remains untouched by this method of investigation; in our studies we reckon with the living properties of an organic body as with a fact which we indeed have not explained, but which is none the less established.

The adherents of the new school, however, believe that they are able to conduct this latter problem to its final solution if they apply the method which they have chosen, of referring everything that happens in the animal body to physico-chemical laws. But every animal body is the result of two groups of forces, which form and transform it. The one is still unexplained, and was formerly termed vital force, the other is the totality of the physico-chemical forces of the outer world. In order to reach the goal which they are striving after, the representatives of the new school completely ignore the fact that in each organism, in each of its cells, processes take place which we term life and cannot explain.

Herein, therefore, lies the great error of the mechanico-etiological school, in believing that it is able to explain life itself, while, on the contrary, its final aim can only be to show how organic formations which are already in existence are subject to the physico-chemical forces just as much as the inorganic bodies. The new element which the mechanico-

etiological school brings with it is therefore false; the true portion of it has long been known as physiology.

In spite of this it is of great importance to lay especial emphasis upon it; it was able to render our historic method considerably more profound, and must become an integral part of phylogenetic investigation. To bring it into a mutually exclusive opposition to the historic method, as has been done, is without justification. Without the idea of descent the structure of an animal body cannot be understood. One example will suffice. In the whalebone whales teeth appear in the earliest embryonic period. These do not cut the gum, are entirely functionless, and after some time, still in the embryo, are completely absorbed. Now how can we succeed in understanding this phenomenon by means of the mechanico-etiological method? Is not our want of a cause satisfied to a certain extent if, on the basis of phylogenetic investigation, we are able to prove that the germs of these teeth are inherited from ancestors of the whalebone whales, in which the teeth were functional, while in the existing whales, in consequence of an altered mode of life, they are replaced by more practical organs in the shape of the whalebone?

In conclusion I would emphasize the fact that I too am convinced that the processes which are termed vital force obey the same laws which dominate the inorganic world. I too behold in the introduction of a vital force, which is to us obscure and mysterious, only an unnecessary addition, and consider the tracing of life to physico-chemical laws, although not as a fact that has been proved, nevertheless as a scientific postulate.

XLII.—*Additions to the Shell-Fauna of the Victoria Nyanza or Lake Oukéréwé.* By EDGAR A. SMITH.

SINCE the publication of my report on the shells of this lake in the 'Annals' for last August I have discovered that Dr. E. von Martens a month or two previously had described five species from the same locality, namely one species of *Limnæa*, a *Physa*, and three species of *Viviparus*. The *Physa* is the species which in his former paper (SB. Gesell. nat. Freund. Berlin, 1879, p. 103) he considered might possibly belong to *P. nyassana*, Smith.